

HABITAT SELECTION IN WOODLAND NEARCTIC–NEOTROPIC MIGRANTS ON THE ISTHMUS OF TEHUANTEPEC I. AUTUMN MIGRATION

KEVIN WINKER^{1,2}

ABSTRACT.—The distribution of autumn migrants among Neotropical wooded habitats was examined using mist nets in a rainforest region of southern México. Capture distributions and local movements from north and south (as reflected by net captures) were examined in 17 species. All species showed significant nonrandom distributions. Captures from the north were not more frequent than expected by chance. Local diurnal movements, therefore, do not reflect the known latitudinal movements occurring in these species, which makes it unlikely that local habitat use is simply the result of directional wandering. Although 65% of captured individuals were first-year birds having no previous experience with tropical rainforest, capture distributions suggested species-specific selectivity to a rather high degree. Also, in the 10 species with adequate sample sizes, distributions between early- and later-day captures tended to be remarkably constant. Habitat selection in these species may be largely endogenous. *Received 30 Nov. 1993, accepted 25 Sept. 1994.*

Habitat selection in birds has long been an important area of study (see Hildén 1965, Cody 1985). The postbreeding, pre-wintering movements of migrant species brings a different aspect to this field, however. The high degree of transience found at this time can result in the co-occurrence of species which overlap neither in breeding nor in wintering ranges in habitats that are unsuitable for either. Further, although small migrants probably need to deposit fat for migration at sites between their breeding and wintering ranges (see Nisbet et al. 1963, Berthold 1975, Bairlein 1987, Winker et al. 1992a), their ability to store energy and their sheer mobility suggest that they may not depend upon food resources in all of the habitats where they occur during migration.

Questions regarding community structure, coexistence, and niche breadth thus take on new dimensions at migratory stopover sites. Habitat selection and use, key components of these questions, have hardly begun to be examined in migration (see Parnell 1969; Berthold et al. 1976; Bairlein 1981, 1983; Hutto 1985a; Berthold 1989; Moore et al. 1990; Winker et al. 1992a, b). They have not been examined at stopover sites in the Neotropics.

This study addresses basic questions of habitat selection among migrants at a Neotropical site in southern México. Are wooded habitats used indiscriminately as they are encountered by migrants or does selection

¹ Conservation and Research Center, NZP, Smithsonian Institution, Front Royal, Virginia 22630.

² Present address: National Museum of Natural History, Division of Birds, Smithsonian Institution, Washington, D.C. 20560.

occur? What is the nature of selection, if it occurs? Do migrants sample the available macrohabitats, then gradually settle in suitable areas? The area chosen to study these questions, the Isthmus of Tehuantepec, is the northernmost narrowing of the North American continental landmass. This region theoretically causes a funneling and concentration of Nearctic–Neotropical landbird migrants, making it likely that stopover sites are heavily used. It also contains the northernmost Neotropical rainforest (Pennington and Sarukhán 1968). Thus, first-year autumn migrants on the Isthmus have no previous exposure to woodlands of this type. Examining the diurnal distributions of these nocturnal migrants under such conditions can give insight into whether habitat selection is, in part, an endogenous phenomenon (e.g., Bairlein 1981, 1983; Berthold 1989).

STUDY SITE AND METHODS

The study site is located just south of the Estación de Biología Tropical “Los Tuxtlas” of the Instituto de Biología of the Universidad Nacional Autónoma de México (UNAM), in the Sierra de los Tuxtlas, southern Veracruz, México (18°34′30″N, 95°04′20″W). This area occupies the NW region of the Isthmus of Tehuantepec. The site is located near the coast of the Gulf of México. It is 5 km S and 3 km W of the coastline, which in this area runs approximately NNW–SSE.

Thirty-six standard nylon mist nets (12 × 2.6 m) were placed 30 m apart in an area offering mature and second growth wooded habitats. Nets were oriented in an E–W direction. This orientation was chosen to enable the detection of diurnal movement inland from the coast (i.e., from the NE), or along the axis of normal diurnal migration in this area (from the NW–N). It is assumed that the side upon which the bird entered the net indicates (on a gross scale) the direction of local movement before capture. The site was composed of primary forest (selva) bordered by second growth woodland (acahual), which in turn changed gradually into old pasture (not sampled). Nets were set in the woodlands, with half in primary forest and half in second growth. These woodlands were not homogeneous, however, and analyses presented consider both the macro- and microhabitat scales. Nets were opened whenever weather permitted during daylight hours, and 12,608 net-h were accumulated between 5 September and 15 November 1992. Sample effort was equal among all nets. When removing birds from nets, the time, net, and side of capture (N or S) were recorded for every individual.

Vegetation analysis was conducted at each net site, following the methods of James and Shugart (1970) with the slight modifications outlined by Winker et al. (1992b). However, the analysis was structural only—species composition was not considered (see Appendix I).

Shortfalls of the methodology.—In a study like this, mist nets sample a non-uniform, three-dimensional space in a relatively uniform manner. In low second growth, the vertical vegetative stratum is fully sampled, while in tall primary forest, nets sample only a small part of this stratum. Species are adequately sampled when their activities are typically in the understory or near the ground. Species whose activities occur in and near the canopy will probably show a biased capture distribution, with relatively more captures occurring in low-stature vegetation. Thus, captures in some species may not reflect that species' macrohabitat distribution. For these reasons, I do not discuss optimal or preferred habitats, believing that such determinations require additional data.

There is a positive aspect to this problem, however. Obtaining a relatively uniform, largely

two-dimensional sample of a three-dimensional environment, without collapsing these three dimensions into two, gives better resolution when comparing spatial distributions among species. For example, in the sampling scheme used in this study, netting data can detect a difference between the distributions of a canopy and ground-level species that might not be apparent with an approach (e.g., censusing) that collapses the third dimension. Of course, our understanding of bird distributions among habitats would be much improved if we could acquire two-dimensional samples from higher levels in the third dimension.

Data analysis.—To examine characteristics of capture distributions, abundance differences among species were eliminated by standardizing the captures at each net to represent the percentage of total captures of each species. Recaptures were ignored. Some explanation of the statistical methods used are in order: *G-test with Williams' correction*. When used with unstandardized side-of-capture data, this test examines whether more captures occurred due to local N-S or S-N movement than would be expected by chance. It is also used to compare early and later-day capture distributions between macrohabitat types. *Cluster analysis (UPGMA method)*. This test is used to depict graphically similarities among net locations according to the structure of the surrounding vegetation (Fig. 1, Appendix) and among species' capture distributions (Fig. 2). Clustering nets on the basis of vegetation structure (see Fig. 1) revealed three groups: primary forest, second growth, and a single outlier. Because the outlier was in primary forest, it is included in this group for macrohabitat comparisons. *Kolmogorov-Smirnov test for "uniform" distribution*. This tests whether the distribution of captures might have come from a population uniformly distributed among capture points. Capture distribution is compared against random numbers taken from a distribution of values uniformly distributed between zero and the maximum percentage of total captures occurring among the nets for a particular species. Significant departure from random "uniformity" (when sample effort is uniform) suggests nonrandom distribution. *Kolmogorov-Smirnov 2-sample test, comparing capture distributions between species pairs*. This test compares the shapes of the distributions of standardized captures among the habitat array. It answers the question of whether distributions differ between species pairs. *Sign test*. As long as one uses standardized data, this test examines a different aspect of the question of how species are similar or dissimilar in their capture distributions. In this case, it essentially tests for differences between species in the breadth of occurrence among the 36 possible capture points. For example, species very dissimilar in two-dimensional distribution (e.g., one occurs largely in primary forest, the other in second growth) may be similar in the specificity or generality of their distributions. As will be seen, differences in distribution must be rather strong to be significant, using this test. Differences were significant when one of the two species occurred with a greater or lesser relative frequency (percentage of total captures) at about 70–80% of the total number of nets at which both species occurred. For example, a comparison of species *a* and *b* would show a significant difference if species *a* occurred with greater relative frequency at 75% of the total nets at which both species occurred.

RESULTS

Seventeen species were chosen for analysis based on their capture frequencies (see Table 1; $N = 1442$ individuals). The percentage of captures occurring from birds entering nets from the north ranged from 44.1% (Worm-eating Warbler, WEWA) to 72.4% (Swainson's Thrush, SWTH; Table 1), averaging 53.3% over all of the captures of these species (all scientific names are in Table 1). Despite the high percentage of captures

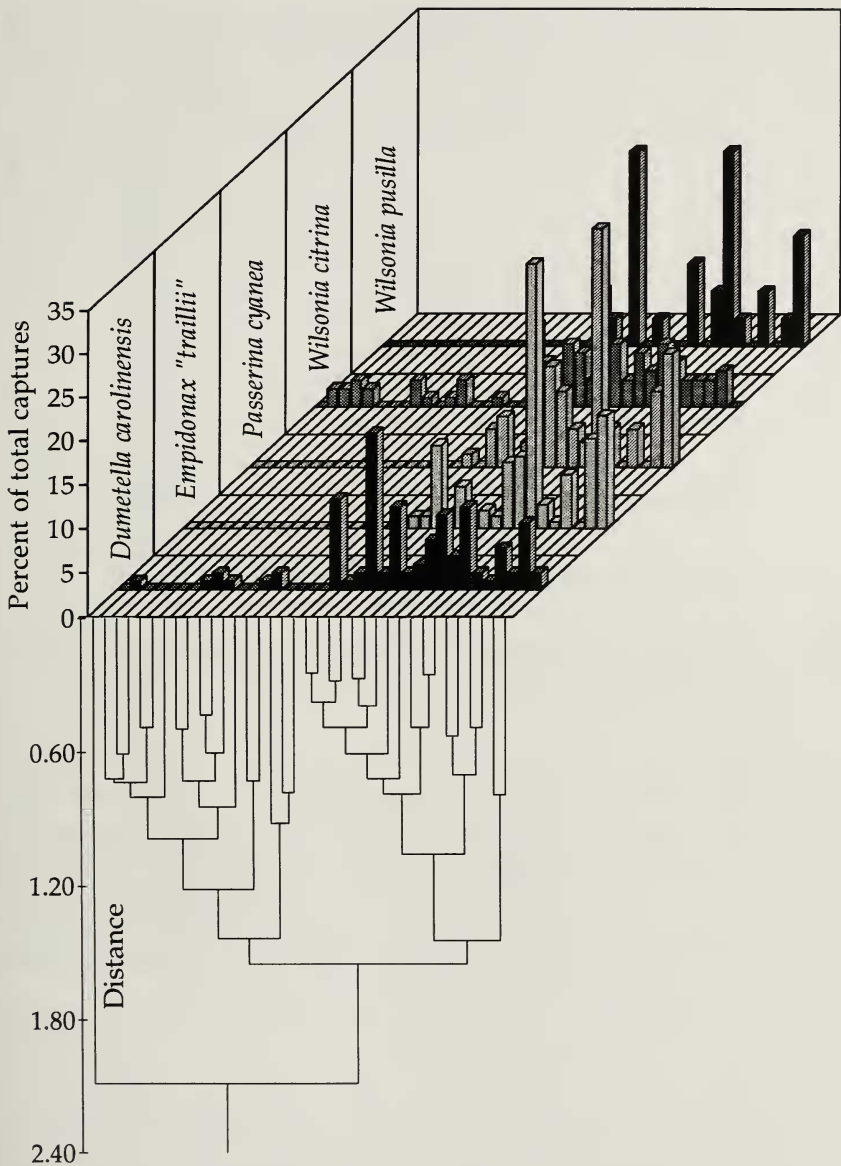


FIG. 1. Relationships among the 36 net locations in vegetation structure (dendrogram) and the capture distributions among these nets of five species that are well sampled using mist nets. The rightmost cluster of 18 locations is second growth; the remainder are primary forest.

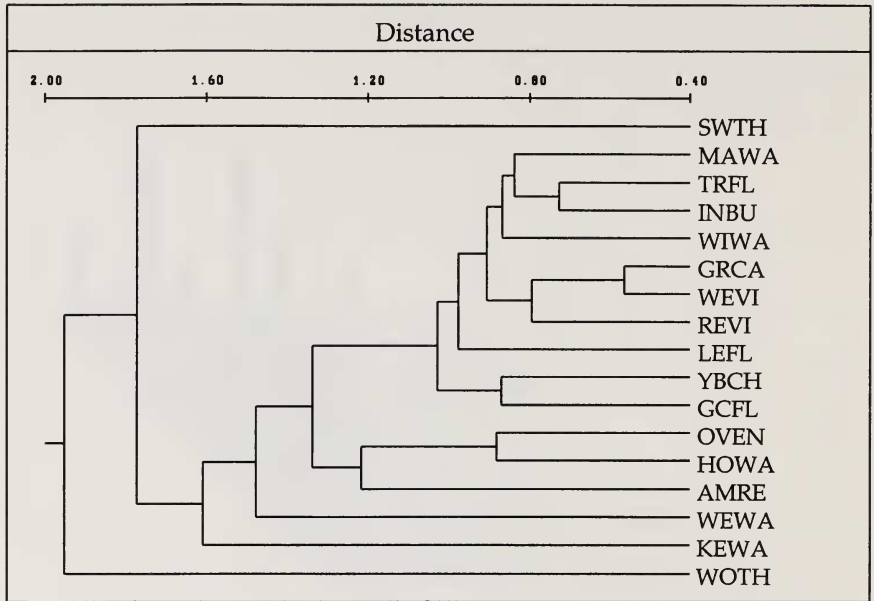


FIG. 2. Dendrogram of similarities in capture distributions among 17 migrant species (UPGMA clustering method). Name codes are in Table 1.

from the north in Swainson's Thrush (clearly an outlier; see Table 1), movements (as reflected in side-of-capture data) were not significantly different from random in any species (Table 1). The local, diurnal movements of the captured individuals, therefore, do not reflect the directional movements that we know are occurring on a seasonal, latitudinal scale. This realization has important consequences from the perspective of habitat selection: The vast majority of captured individuals are not occurring in the available habitats as a result of directional wandering.

If local captures do not reflect the seasonal direction of movement, there is a greater possibility that an individual's presence in a particular habitat is due to factors other than the simple fact that the habitat patch lies between the individual and its destination. Are such factors operating? This can be answered by determining whether individuals are distributed randomly among the available habitats. All of the 17 species examined showed highly significant nonrandom capture distributions (Table 1; Kolmogorov-Smirnov test against a random "uniform" distribution; $P < 0.001$). Habitat selection, therefore, seems to occur in all of the species examined.

If migrants were sampling available macrohabitats, then gradually set-

TABLE 1

SAMPLE SIZES OF COMMON MIGRANTS AND CAPTURE PERCENTAGES OCCURRING ON THE NORTH SIDE OF THE NETS, WITH RESULTS OF STATISTICAL TESTS EXAMINING DIRECTIONALITY (G -TEST) AND CAPTURE DISTRIBUTIONS^{a,b}

Common name	Scientific name	Namecode	N	%	G_{adj}^b	P^b	Z^c	P^c
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	GCFL	46	56.5	0.39	$0.9 > P > 0.5$	4.00	0.000
"Trail's" Flycatcher	<i>Empidonax "trilliti"</i>	TRFL	148	55.4	0.86	$0.5 > P > 0.1$	4.13	0.000
Least Flycatcher	<i>E. minimus</i>	LEFL	32	56.3	0.25	$0.9 > P > 0.5$	3.98	0.000
Gray Catbird	<i>Dumetella carolinensis</i>	GRCA	107	49.5	0.00	$1.0 > P > 0.9$	3.77	0.000
Wood Thrush	<i>Hylocichla mustelina</i>	WOTH	60	58.3	0.83	$0.5 > P > 0.1$	2.13	0.000
Swainson's Thrush	<i>Catharus ustulatus</i>	SWTH	29	72.4	3.02	$0.1 > P > 0.05$	2.82	0.000
White-eyed Vireo	<i>Vireo griseus</i>	WEVI	140	53.6	0.36	$0.9 > P > 0.5$	3.64	0.000
Red-eyed Vireo	<i>V. olivaceus</i>	REVI	273	48.0	0.22	$0.9 > P > 0.5$	3.54	0.000
Magnolia Warbler	<i>Dendroica magnolia</i>	MAWA	83	54.2	0.29	$0.9 > P > 0.5$	3.57	0.000
American Redstart	<i>Setophaga ruticilla</i>	AMRE	51	54.9	0.24	$0.9 > P > 0.5$	3.00	0.000
Worm-eating Warbler	<i>Helminthos vermivorus</i>	WEWA	34	44.1	0.23	$0.9 > P > 0.5$	3.47	0.000
Ovenbird	<i>Seiurus aurocapillus</i>	OVEN	110	60.0	2.21	$0.5 > P > 0.1$	2.24	0.000
Kentucky Warbler	<i>Oporornis formosus</i>	KEWA	87	52.9	0.14	$0.9 > P > 0.5$	2.50	0.000
Hooded Warbler	<i>Wilsonia citrina</i>	HOWA	97	52.6	0.13	$0.9 > P > 0.5$	2.34	0.000
Wilson's Warbler	<i>W. pusilla</i>	WIWA	31	45.2	0.14	$0.9 > P > 0.5$	4.17	0.000
Yellow-breasted Chat	<i>Icteria virens</i>	YBCH	45	46.7	0.10	$0.9 > P > 0.5$	4.00	0.000
Indigo Bunting	<i>Passerina cyanea</i>	INBU	69	59.4	1.22	$0.5 > P > 0.1$	4.05	0.000

^a Captures from the north were no higher than expected by chance. In contrast, capture distributions are all significantly different from random "uniform" distributions.

^b G -test with Williams' correction; associated G - and P -values; see Sokal and Rohlf (1981).

^c Kolmogorov-Smirnov goodness of fit test against the uniform distribution; associated Z - and P -values.

ting in suitable patches, there should be differences between early- and later-day macrohabitat distribution patterns. Sample sizes were not suitable for this analysis in all species. Among the 10 species with ≥ 60 individuals captured, none showed differences between early- ($<10:01$ h) and later-day ($>10:01$ h) capture distributions in primary forest and second growth (G -test with Williams' correction; $G_{\text{adj}} > 0.10$). Thus, patterns of capture at the macrohabitat level do not seem to change during the day.

At the microhabitat level, changes in distribution during the day might be expected under some conditions. Less-preferred areas, or areas that were not harvested in the morning, may be preferred later in the day. Also, diurnal changes in prey availability, or prey-switching, could cause microhabitat shifts. I have observational data (unpubl.) suggesting both of these may occur among migrants foraging at a stopover site in Minnesota (autumn 1987), but to my knowledge these spatial shifts have not been documented quantitatively in woodland birds (although they occur in wintering shorebirds; see Connors et al. 1981). Analysis of distributions on a microhabitat scale (net-by-net) between early- ($<10:01$) and later-day ($>10:01$) captures revealed a significant change in only one species of the ten in which 60 or more individuals were captured. The Kentucky Warbler (KEWA) showed a significant shift in capture distributions between early- and later-day captures (Kolmogorov-Smirnov two-sample test; $P = 0.037$). The other nine species examined were remarkably constant in their distributions between these periods (same test; $P > 0.5$).

It is apparent that distributions can differ markedly among species (Fig. 1). While species may theoretically exist in relative separation in multi-dimensional niche space, it is highly unlikely that an array of 36 mist nets sampling two physical dimensions can detect much of this separation, even if it exists. Despite this unlikelihood, of the 136 possible between-species comparisons, fully 40 (29.4%) showed significant differences in distribution (Table 2). This seems a rather high degree of species-level differentiation in how individuals are distributed within the available habitat array.

A cluster dendrogram of similarities in distributions among species (Fig. 2) reveals groupings that might have been roughly predicted, given an understanding of these species in the field. The natural cluster of species from Magnolia Warbler (MAWA) to Great Crested Flycatcher (GCFL) constitutes a group whose captures occurred primarily (and in some cases exclusively) in second growth woodland. The grouping of the Magnolia Warbler with "Traill's" Flycatcher (TRFL) and the Indigo Bunting (INBU) is probably inaccurate with respect to macrohabitat use. While this grouping accurately reflects distributions in sampled space,

Magnolia Warblers (unlike “Traill’s” Flycatchers and Indigo Buntings) regularly occur in primary rainforest; their activity levels in this habitat tend to be nearer the canopy than at net levels, however (pers. obs.). The foraging levels of White-eyed (WEVI) and Red-eyed vireos (REVI), Wilson’s (WIWA) and Worm-eating warblers (WEWA), and the American Redstart (AMRE) also tend to be higher in primary forest, making their exact position in Fig. 2 from the macrohabitat perspective unclear. Although Fig. 2 is useful for a broad-brush view of interspecific distributional relationships, Table 2 more accurately depicts real differences.

Another question of habitat selection is whether distribution is narrow or broad with respect to the sampled habitats. This aspect was examined using the sign test (see Methods), and the results, as expected, show fewer differences between species pairs (approximately 9% of all pairwise comparisons) than the Kolmogorov-Smirnov two-sample test (Table 2). The differences (see Table 2) tended to occur between species whose captures were widely distributed among the sampled habitats (e.g., Wood Thrush [WOTH], Swainson’s Thrush, Ovenbird [OVEN], Hooded Warbler [HOWA], Kentucky Warbler), and species whose captures occurred primarily in younger second growth (“Traill’s” Flycatcher [TRFL], Wilson’s Warbler, Yellow-breasted Chat [YBCH], Indigo Bunting).

Of the 1339 individuals whose age was determined with certainty, 64.97% were immature, or first-year birds.

DISCUSSION

Coexistence among species in stable avian communities (e.g., breeding, wintering) occurs because individuals of each species are able to exploit different aspects of locally available resources (resource dimensions of the niche). In multidimensional niche space, each species in a stable community would occupy its own general area. This may not be true of migrants at stopover sites because of the ephemerality of these communities and the possibility that local resources are not needed or used by some of the communities’ temporary members. Given also that more species occur at a stopover site during the migratory period than at any other time, there is great potential for species overlap in niche space. We do not know the degree to which this multidimensional space may or may not be “partitioned.”

Bairlein (1981, 1983) found evidence for species-level segregations corresponding to morphology at a Palearctic stopover site. The array of habitats sampled in my study is much narrower, however, and at a finer scale (within woodlands), we should expect results to be more ambiguous, particularly when the mist net is the tool used to examine distributions. In an array of only 36 nets, we expect that some species will show similar

TABLE 2
RESULTS OF STATISTICAL TESTS EXAMINING STANDARDIZED CAPTURE DISTRIBUTIONS BETWEEN SPECIES PAIRS^a

	GCFL	TRFL	LEFL	GRCA	WOTH	SWTH	WEVI	REVI	MAWA	AMRE	WEWA	OVEN	KEWA	HOWA	WIWA	YBCH	INBU
GCFL	—	n.s.	n.s.	*	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	**	**	n.s.	n.s.	n.s.
TRFL	n.s.	—	n.s.	n.s.	**	*	n.s.	n.s.	n.s.	n.s.	n.s.	*	**	**	n.s.	n.s.	n.s.
LEFL	n.s.	n.s.	—	n.s.	*	*	n.s.	n.s.	n.s.	n.s.	n.s.	*	**	*	n.s.	n.s.	n.s.
GRCA	n.s.	n.s.	n.s.	—	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	*	n.s.	n.s.
WOTH	n.s.	*	n.s.	n.s.	—	n.s.	**	**	*	n.s.	n.s.	n.s.	n.s.	n.s.	**	*	**
SWTH	n.s.	n.s.	n.s.	n.s.	n.s.	—	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	*	*	n.s.
WEVI	n.s.	*	n.s.	n.s.	n.s.	n.s.	—	n.s.	n.s.	n.s.	n.s.	n.s.	*	*	n.s.	n.s.	n.s.
REVI	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	—	n.s.	n.s.	n.s.	*	**	*	n.s.	n.s.	n.s.
MAWA	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	—	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
AMRE	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	—	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
WEWA	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	—	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
OVEN	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	—	n.s.	n.s.	**	*	*
KEWA	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	—	n.s.	***	**	**
HOWA	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	—	**	*	*
WIWA	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	*	*	*	*	n.s.	n.s.
YBCH	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	—	n.s.	n.s.
INBU	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.

^a Above the diagonal are the results of a Kolmogorov-Smirnov 2-sample test, testing for differences between species' distributions on a net-by-net basis. Below the diagonal are the results of a sign test, which tests for differences in capture distributions by comparing, essentially, the breadth of occurrence among the 36 nets. See text. Names corresponding to species codes are given in Table 1. * = $P < 0.05$; ** = $P < 0.01$; *** = $P \leq 0.001$.

^b $P = 0.054$.

distributions, regardless of whether they are coexisting under a regime of differential resource exploitation or whether they are simply co-occurring. Species which in this study appear similar in two-dimensional distribution may occupy different niche space, but determination of this will require consideration of other data, such as diet, foraging maneuvers, height of activity, etc. Observations of the species considered here (unpubl.) suggest that such differences exist and can be quantified. There is also some temporal segregation (e.g., the Kentucky Warbler is an early migrant, while the Wood Thrush is later). These are only 17 of the 137 species captured in autumn at this site, however, leaving a tremendous degree of complexity unconsidered in this avian community.

Selectivity.—It is possible that some migrants do not feed at a site, occupying only physical, three-dimensional space and not casting a shadow upon the resource dimensions of the local environment. This may occur, for example, in migration “waves,” when large numbers of birds can be found at a site, often apparently not feeding (although evidence remains anecdotal). If individuals were not consuming resources, there would be little pressure to seek profitable foraging locations, and any selection existing would be due to factors such as predator avoidance, temperature, humidity, etc. Under this scenario, we should expect broad distributions among wooded habitats in woodland birds, with much overlap between species. The evidence considered here suggests that this type of situation is not occurring at this site, but that, instead, a rather high degree of species-specific distribution occurs (Table 2, Fig. 2). Other evidence from this site (Winker 1995) suggests that resource demand probably drives a considerable amount of the selectivity observed.

The nature of the selection.—Hutto (1985b) suggested that exploratory assessment of nonbreeding habitats may occur among migrants at the landscape and macrohabitat scales. The data considered here do not address the landscape level, but the lack of evidence for shifting distributions at the macrohabitat scale suggests that exploratory assessment is either very rapid (occurring on a time scale not detectable using mist nets opened at dawn) or limited to finer scales. We know that assessment occurs in migrants at stopover sites. Both intraseasonal (Bairlein 1981, 1983) and interseasonal (e.g., Hutto 1985a; Winker et al. 1992a, b) changes in distribution suggest resource tracking (although interseasonal changes may be intertwined with endogenous selection criteria which themselves change seasonally). The within-day microhabitat distributional changes found at this site in the Kentucky Warbler are probably due to fine-scale resource tracking. On average, individuals of this species are gaining mass during the day at this site, and they seem to be depositing small to moderate amounts of fat (Winker 1995).

The lack of significant directionality in local movement (as reflected by side-of-capture data) corresponds well with my observations. Directional movements were commonly observed during the day in diurnal migrants of the families Accipitridae, Cathartidae, Apodidae, Columbidae, and Hirundinidae, but not among nocturnal migrants (unpubl. data). The absence of evidence for macrohabitat sampling and subsequent settling corresponds with stopover data in Germany (Bairlein 1981, 1983; Berthold 1989) and also supports my field observations. Despite hundreds of hours of observation in this area during autumn migration, I have not seen behaviors suggesting macrohabitat switching (or sampling and settling) as described by other investigators (e.g., Moore et al. 1990, Wiedner et al. 1992). This result underscores the likelihood that migrants can behave differently when right on the Atlantic coast (as opposed to even slightly inland, as at this site).

The question of endogeneity.—The majority of captured individuals were in their first year, and had never experienced tropical rainforest. Yet a rather high degree of species-specific selectivity occurred among the available habitats. This, coupled with the fact that distributions tended not to change during the day, leads me to conclude that habitat selection in these species may be largely endogenous.

Choices of where to settle appear to be made very quickly; the process was not apparent in observational or netting data. Also, potential exposure to social factors during the day (e.g., learning) did not seem to cause distributional shifts. Apparently rapid selection, comparative stability in distribution during the day, and species-specific patterns were all found here in non-flocking, relatively inconspicuous birds, the majority of which were naive or inexperienced. Similar results at a stopover site in Germany led Bairlein (1981, 1983) and Berthold (1989) to conclude that habitat selection in many Palearctic-Paleotropical migrants was probably under endogenous control. This control is not entirely rigid, however. Bairlein (1983) found evidence that young birds were distributed somewhat differently than adults in two species. He surmised that although habitat selection may be largely innate in passerine migrants, some part of this selection process may be improved by learning. In this context it is interesting to note that in my study within-day change in microhabitat distribution occurred in only one species.

Habitat selection in migrants.—Perhaps because little work has been done on migrant habitat selection, there is disagreement about how these studies should proceed. For example, I suggest that Wiedner et al.'s (1992) recommendations regarding the study of habitat selection in transient migrants (e.g., beginning data gathering 2–3 h after sunrise) are premature. First, the phenomenon they describe—flights of nocturnal migrants ex-

tending well into daylight hours—probably occurs primarily near large ecological barriers. Secondly, waiting 2–3 h after sunrise to begin examining the distribution of individuals causes one to miss the most active period. The data-gathering and analytical methods used here (directionality and comparisons of distributions between different times of day) can adequately address the question of settling.

The important issue in migrant habitat selection, however, is whether (or to what degree) transient migrants are actually *using* available stop-over habitats. The idea that migrant habitat selection can be adequately studied through censusing alone ignores the uniqueness of the stopover community: namely, high levels of mobility, the ability to store energy, and the consequent possibility of not being dependent upon a site for food resources. The abundance of a species occurring at a site does not appear to be correlated with the importance of a site for fat deposition (see Winker et al. 1992c, Winker 1995). Further, remarkable differences in apparent resource harvesting can occur among the most common species at a site (Winker et al. 1992c). Learning about and accounting for the differences that appear among these species will be crucial both for an understanding of the evolution of the Nearctic–Neotropic migration system and for the successful conservation of this diverse group.

ACKNOWLEDGMENTS

The Smithsonian Institution and the Chicago Zoological Society supported the study. G. de la Garza (SEDUE), Dr. E. Ezcurra (SEDESOL), and G. Pérez H. (Estación de Biología Tropical “Los Tuxtlas,” Instituto de Biología, UNAM) kindly issued the necessary permits. F. Puebla provided excellent field assistance. R. L. Hutto, P. Kerlinger, M. V. McDonald, and J. H. Rappole gave helpful comments.

LITERATURE CITED

- BAIRLEIN, F. 1981. Ökosystemanalyse de Rastplätze von Zugvögeln: Beschreibung und Deutung der Verteilungsmuster von ziehenden Kleinvögeln in verschiedenen Biotopen der Stationen des “Mettnau-Reit-Ilmütz Programmes. *Ökol. Vögel* 3:7–137.
- . 1983. Habitat selection and associations of species in European passerine birds during southward, post-breeding migrations. *Ornis Scand.* 14:239–245.
- . 1987. The migratory strategy of the Garden Warbler: a survey of laboratory and field data. *Ringling & Migr.* 8:59–72.
- BERTHOLD, P. 1975. Migration: control and metabolic physiology. Pp. 77–128 in *Avian biology*, Vol. 5 (D. S. Farner and J. R. King, eds.). Academic Press, New York, New York.
- . 1989. The control of migration in European warblers. *Intern. Congr. Ornithol.* 19: 215–249.
- , F. BAIRLEIN, AND U. QUERNER. 1976. Über die Verteilung von ziehenden Kleinvögeln in Rastbiotopen und den Fangerfolg von Fanganlagen. *Vogelwarte* 28:267–273.
- CODY, M. L. 1985. *Habitat selection in birds*. Academic Press, San Diego, California.
- CONNORS, P. G., J. P. MYERS, C. S. W. CONNORS, AND F. A. PITELKA. 1981. Interhabitat

- movements by Sanderlings in relation to foraging profitability and the tidal cycle. *Auk* 98:49–64.
- HILDÉN, O. 1965. Habitat selection in birds: a review. *Ann. Zool. Fenn.* 2:53–75.
- HUTTO, R. L. 1985a. Seasonal changes in the habitat distribution of transient insectivorous birds in southeastern Arizona: competition mediated? *Auk* 102:120–132.
- . 1985b. Habitat selection by nonbreeding, migratory landbirds. Pp. 455–476 in *Habitat selection in birds* (M. L. Cody, ed.). Academic Press, San Diego, California.
- JAMES, F. C. AND H. H. SHUGART, JR. 1970. A quantitative method of habitat description. *Audubon Field Notes* 24:727–736.
- MOORE, F., P. KERLINGER, AND T. R. SIMONS. 1990. Stopover on a Gulf coast barrier island by spring trans-Gulf migrants. *Wilson Bull.* 102:487–500.
- NISBET, I. C. T., W. H. DRURY, JR., AND J. BAIRD. 1963. Weight loss during migration. Part I: Deposition and consumption of fat in the Blackpoll Warbler *Dendroica striata*. *Bird-Banding* 34:107–139.
- PARNELL, J. F. 1969. Habitat relations of the Parulidae during spring migration. *Auk* 86:505–521.
- PENNINGTON, T. D. AND J. SARUKHÁN. 1968. *Arboles tropicales de México*. Inst. Nac. Invest. Forestales, México.
- SOKAL, R. R. AND F. J. ROHLF. 1981. *Biometry*, second ed. W. H. Freeman, San Francisco, California.
- WIEDNER, D. S., P. KERLINGER, D. A. SIBLEY, P. HOLT, J. HOUGH, AND R. CROSSLEY. 1992. Visible morning flight of Neotropical landbird migrants at Cape May, New Jersey. *Auk* 109:500–510.
- WINKER, K. 1995. Autumn stopover on the Isthmus of Tehuantepec in some woodland Nearctic–Neotropical migrants. *Auk* 112:000–000. (in press)
- , D. W. WARNER, AND A. R. WEISBROD. 1992a. The Northern Waterthrush and Swainson's Thrush as transients at a temperate inland stopover site. Pp. 384–402 in *Ecology and conservation of Neotropical migrant landbirds* (J. M. Hagan and D. W. Johnston, eds.), Smithsonian Institution Press, Washington, D.C.
- , ———, AND ———. 1992b. Migration of woodland birds at a fragmented inland stopover site. *Wilson Bull.* 104:580–598.
- , ———, AND ———. 1992c. Daily mass gains among woodland migrants at an inland stopover site. *Auk* 109:853–862.

WILSON ORNITHOLOGICAL SOCIETY ANNUAL MEETING

The Wilson Ornithological Society will hold its annual meeting from 4 to 7 May 1995 at the Fort Magruder Inn and Conference Center in Williamsburg, Virginia. Queries may be directed to: Ruth Beck, Dept. of Biology, College of William and Mary, Williamsburg, Virginia 23185.

APPENDIX I
VEGETATION STRUCTURE OF SAMPLED HABITATS^a

P1	12	2	5	1	0	1	0	0	24	43	90	22
P2	7	9	6	3	0	0	1	0	21	55	80	25
P4	11	7	5	1	1	0	1	0	29	45	75	22
P16	11	11	8	2	1	0	1	0	50	30	90	23
P8	11	3	6	3	0	0	1	0	42	30	90	22
P15	17	2	5	3	1	0	1	0	35	29	81	20
P17	8	7	5	2	1	0	2	0	38	30	90	22
P3	3	7	5	3	0	0	0	0	22	45	65	23
P6	11	5	3	3	0	0	0	0	31	40	80	20
P5	6	7	3	1	1	0	0	0	50	35	80	21
P11	8	4	4	2	1	0	0	0	36	50	80	22
P12	12	7	4	2	2	0	0	0	31	25	80	18.5
P13	16	12	6	3	2	0	0	0	54	45	75	22
P10	4	6	8	1	2	0	0	0	36	55	80	18
P18	10	13	7	0	3	0	0	0	48	70	85	17
P7	8	6	2	0	0	0	1	1	38	40	95	19
P9	5	9	1	2	1	0	0	1	54	50	85	25
P14	17	5	4	1	0	0	0	1	60	55	86	25
A21	20	6	0	0	0	0	0	0	98	70	65	10
A27	23	4	1	0	0	0	0	0	122	70	65	12
A24	16	8	0	0	0	0	0	0	156	65	65	10.5
A25	19	6	0	0	0	0	0	0	167	65	55	7.5
A22	23	10	0	0	0	0	0	0	162	55	75	10.5
A32	23	7	0	0	0	0	0	0	122	50	75	9.5
A38	16	10	1	0	0	0	0	0	130	52	81	13.5
A35	16	11	2	1	0	0	0	0	66	55	60	12
A34	18	2	0	0	0	0	0	0	217	45	60	4.5
A23	14	2	0	0	0	0	0	0	161	70	45	6.5
A28	5	3	1	0	0	0	0	0	136	75	55	7
A30	4	1	0	0	0	0	0	0	131	80	65	6
A31	19	19	1	0	0	0	0	0	123	48	86	13
A36	26	22	3	1	0	0	0	0	92	38	86	14.5
A33	27	13	3	0	0	0	0	0	113	50	68	11.5
A37	30	12	5	0	0	0	0	0	96	38	90	14
A26	6	3	1	0	0	0	0	0	196	95	10	6.5
A29	5	0	0	0	0	0	0	0	344	70	15	5.5

^aColumns are (1) net number; (2-9) number of trees in each size class (A-H); (10) number of "shrub" stems; (11) percent ground cover; (12) percent canopy cover; (13) canopy height (m). Rows (nets) correspond from top to bottom with the dendrogram in Fig. 1 (left to right).